

A Morphometric and Revisionary Study of the Littoral Beetle Genus *Cryptadius* LeConte, 1852 (Tenebrionidae: Coleoptera)

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Abstract.—The tenebrionid genus *Cryptadius* LeConte occurs in littoral habitats of southern California and northwestern Mexico. Through a geographic study of character distribution and a morphometric analysis of population variation, the 9 nominal species of the genus are reduced to 3. *Cryptadius oviformis* Casey, *C. punctipennis* Casey and *C. curvipes* Casey are placed in synonymy under *C. inflatus* LeConte; this species occurs on the Pacific coast of Baja and southern California. *Cryptadius sinuatus* Blaisdell, *C. angulatus* Blaisdell, and *C. andrewsi* Berry are placed in synonymy under *C. tarsalis* Blaisdell; this species occurs on the gulf coast of Baja California. *Cryptadius sonora* Berry, from the Sonoran coast, is retained as valid. *Cryptadius inflatus* is divided into 2 subspecies: *C. i. blaisdelli*, n. ssp. from Baja Sur, and *C. i. inflatus* from southern California.

A morphometric analysis of geographic variation among populations of *Cryptadius* was undertaken as a prelude to a taxonomic revision of the genus. These beetles inhabit the sandy coastal strands of California and northwestern Mexico where the shrubby littoral vegetation approaches the tidal limits. These tenebrionids are flightless and burrow in the sand beneath salt tolerant plants such as saltbush (*Atriplex* spp.) or pickleweed (*Salicornia* spp.), often where the sand is moistened by the high tides or ocean spray. Such habitats are separated by stretches of rocky shoreline, muddy estuaries and unstable, unvegetated beaches, environments unsuitable for *Cryptadius*. In essence therefore, these populations have a disjunctive but linear distribution along some 3000 km of coastline.

Cryptadius at present contains 9 species and has not been the subject of a modern revision. The genus was proposed by LeConte in 1852 to hold a new species, *inflatus*, based on a unique specimen from San Diego, California. Subsequently, this specimen was lost at sea while being sent to Europe for study. For its identity we rely on the authority of Horn (1874) and Casey (1890) who based their descriptions on specimens from the type locality. Casey (1907) redefined *Cryptadius* and proposed 3 new species, all from southern California. Casey distinguished his species primarily by the form of the body which ranged from "broadly-oval" to "oblong-oval," and secondarily by the density of surface punctation, though only in relative terms, i.e., more or less dense than in *inflatus*. Blaisdell (1923) remarked without elaboration that Casey's species were nothing more than *inflatus* and its phases. Blaisdell in his turn added 3 new species to the genus, all from the Baja California peninsula and constructed a key for their separation, later (1943) adding additional locality records. He emphasized differences in the shape of the pronotum, especially the posterolateral angles.

In recent times, Berry (1974, 1977) provided the first descriptions of male genitalia and named 3 new species, 2 from Sonora and 1 from Texas. The Texas species has since been removed to a distinct and separate genus (Thomas, 1984). Berry observed that Blaisdell's flippant dismissal of Casey's species, while possibly correct, should not be accepted without a thorough review of the species. The following report attempts such a review.

METHODS

In addition to specimens borrowed from museums, collecting trips were made to the beaches of southern California, Sonora, and the Baja California peninsula. Beetles were collected live by sieving sand beneath shrubs nearest to the shoreline, the specimens placed immediately into 70% ethanol for preservation. All measurements were made on pinned specimens to the nearest 0.05 mm with the aid of a graduated ocular on a dissecting, binocular microscope at a magnification of $14\times$. It was assumed that beetles of similar morphotype from a single locality were conspecific. At some localities different morphotypes were sympatric. Only localities for which there were at least 10 specimens available were included in the morphometric analyses. Males and females were not considered separately as no secondary sexual characters were found. The mean total body length of 36 females was 6.5 mm while that of 21 males from the same locality was 6.4 mm. This difference was not statistically significant at $P = 0.05$.

Basic statistical functions were performed on a Hewlett-Packard HP-65 programmable calculator. The Student-Newman-Keuls Multiple Range Test (Sokal and Rohlf, 1969) was used to compare sample means.

RESULTS AND DISCUSSION

A search for characters revealed the presence of 3 discrete forms or morphotypes of *Cryptadius*, each morphotype having a distinctive geographical distribution (Fig. 1). A pacific coast morphotype occurs from Point Conception in California to the tip of Baja California at Cabo San Lucas. A peninsula morphotype occurs on the gulf coast of Baja California, many of the gulf islands and on the northern coast of Sonora. A sonoran morphotype occurs on the coast of Sonora from Punta Peñasco south to Guaymas and at one known location on the Baja peninsula. The sonoran and peninsula morphotypes are thus sympatric over a part of their ranges. The 3 forms are distinguished by the shape of the pronotum, especially the posterolateral angles, the shape of the scutellum, and by a combination of other characters which are discussed in the keys and diagnoses that follow. Populations of these morphotypes were analyzed for morphometric heterogeneity.

The Pacific coast morphotype includes *Cryptadius inflatus* of authors and the species described by Casey but considered by Blaisdell to be "phases" of *C. inflatus*. Statistically significant morphometric differences are found among the different populations of this morphotype (Table 1) of which many are of single dimensions in a discordant pattern. A few differences were found to have a distinct geographic pattern. The overall size (both length and width) of the populations in the central part of the range are significantly smaller than those either to the north or the south (Fig. 2). This character reversal correlates with a reversed cline in humidity, the northern Baja coast being more arid than areas to the north or south (Wiggins, 1980). Whether or not there is a cause and effect relationship for

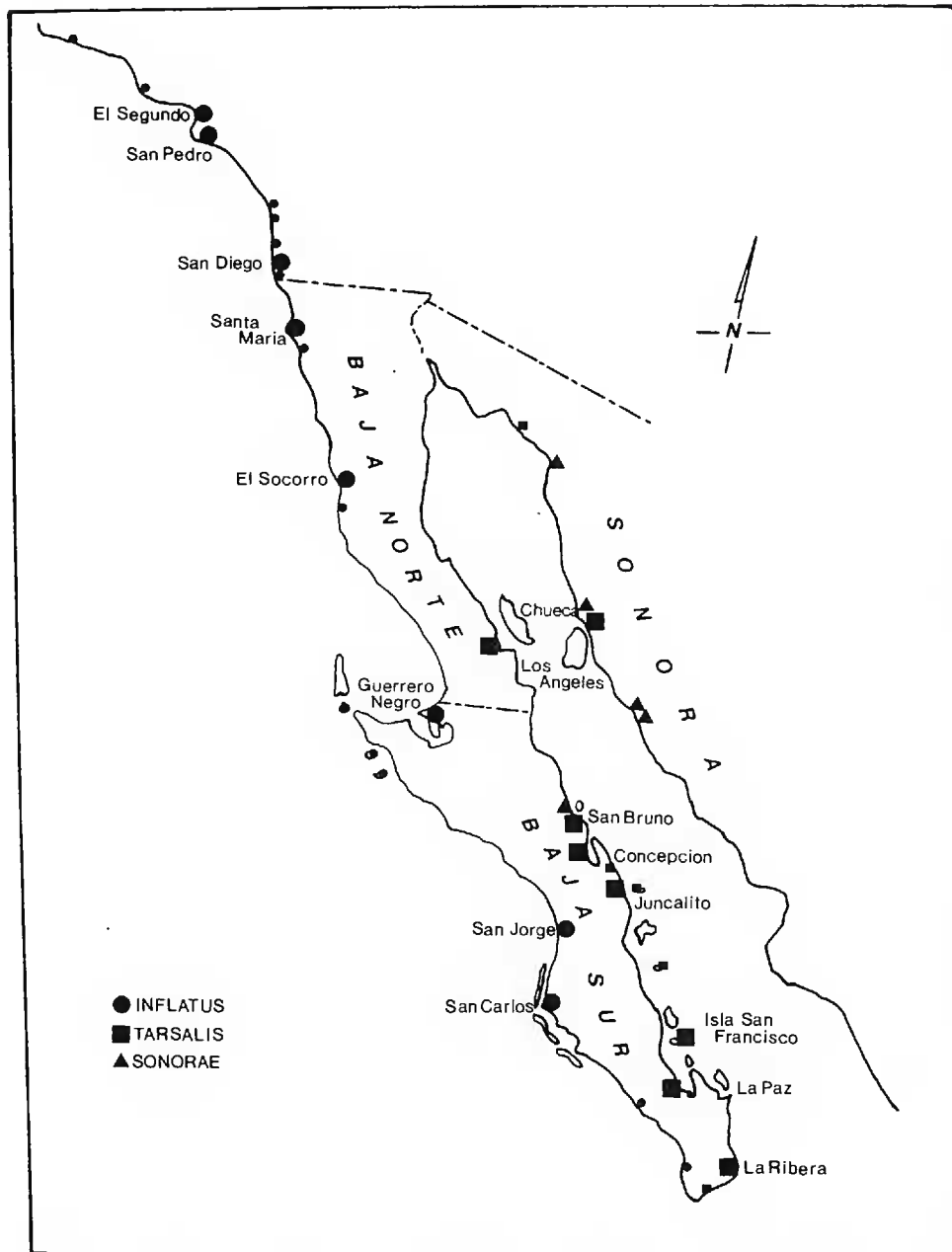


Figure 1. Distribution of *Cryptadius*. Localities included in morphometric analyses indicated by large symbols.

this correlation, the taxonomic significance of this variation is that it magnifies the distinctiveness of the southern populations.

A strong character divergence is found by comparing the proportions of the pronotum between populations from the pacific coast of Baja California Sur with those further north. In the southern populations the pronotal base is proportionately wider. Figure 3 shows the degree of divergence between the forms. While the difference is manifestly and statistically significant and involves a character which is important in distinguishing full species of many tenebrionids, there is still some overlap between the populations. Where the distributions of the populations converge, there is intergradation of the pronotal character. Since the populations cannot be further discriminated by supporting characters I consider these regional forms to be no more than races or subspecies of a single species. All of the Pacific coast populations are therefore assignable to *Cryptadius inflatus* LeConte, divisible into a northern and a southern subspecies.

The peninsula morphotype includes *Cryptadius tarsalis* Blaisdell, *C. sinuatus* Blaisdell, *C. angulatus* Blaisdell, and *C. andrewsi* Berry. While there is somewhat

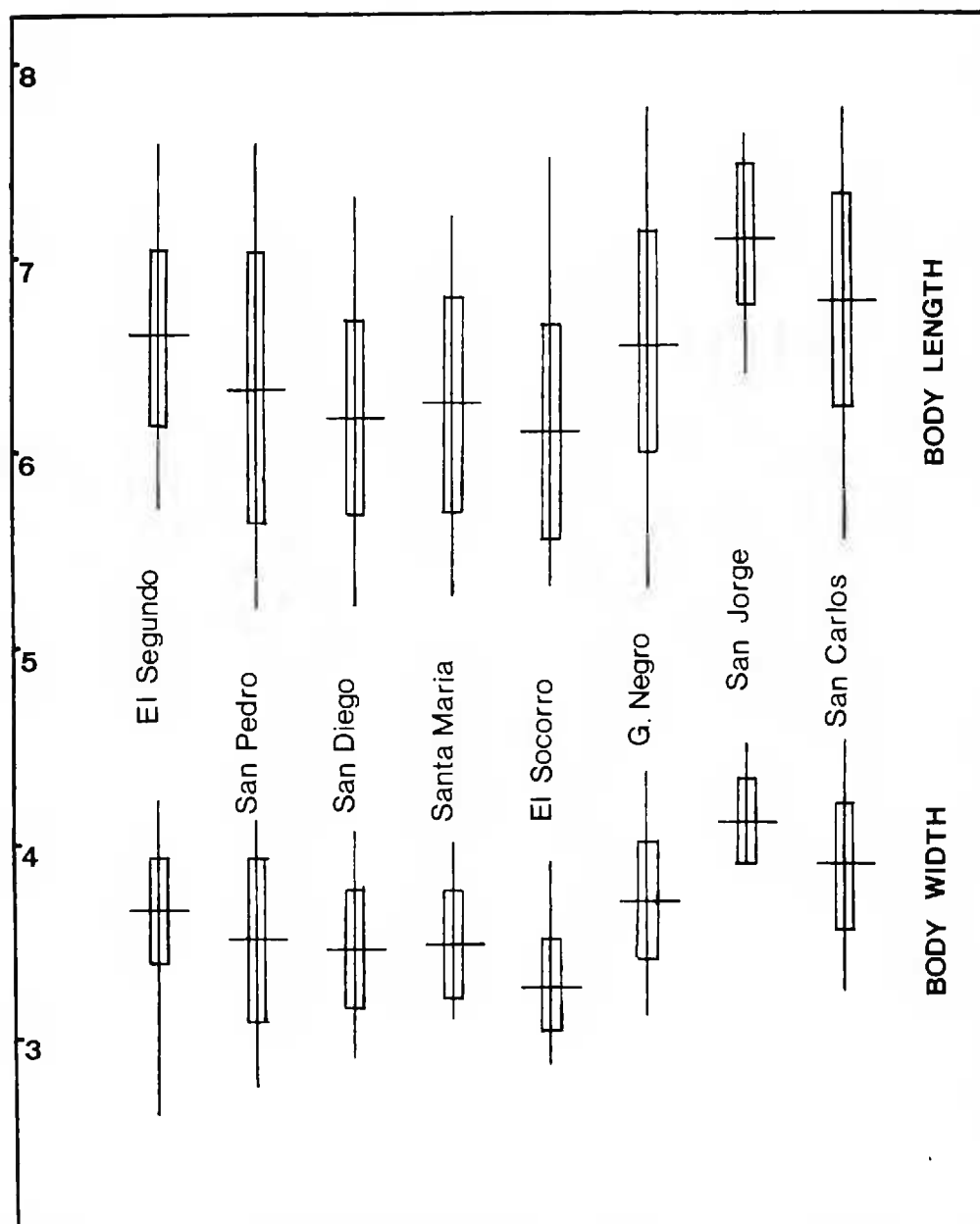


Figure 2. Size variation in pacific coast populations of *Cryptadius inflatus*; mean, range and standard deviation in mm.

less interpopulation variation within this morphotype than in the preceding, there are significant differences in several characters between populations, though not in a congruous geographic pattern. Most of the variation involves size rather than proportion, and it is ironic that the two populations which represent the extremes are from Bahia Concepcion, which Blaisdell named *C. sinuatus*, and Bahia Los Angeles, the type locality for his *C. tarsalis*. It can be seen (Table 2 and Fig. 4) that the size differences between these two populations are filled by the other populations, including *C. andrewsi* from northern Sonora and *C. angulatus* from Carmen Island, in a continuous manner. Since no discrete characters separate these populations, and no morphometric discontinuities are demonstrable, it must be concluded that this morphotype represents a single taxonomic entity. These populations are assigned to *C. tarsalis* Blaisdell.

The Sonoran morphotype is known from 5 localities on the Mexican mainland and one on the Baja California peninsula (Playa San Bruno). Table 3 shows that the degree of intrapopulation variation exhibited by this form is comparable to that seen in the preceding. While there are not enough localities represented in these data for the analysis of interpopulation variation to be definitive, the evi-

Table 1. Morphometric data for Pacific coast populations of *Cryptadius*, localities listed north-to-south. Means and standard deviations in mm. Means without blocks or followed by the same letter are not significantly different at $P = 0.05$.

	El Segundo	San Pedro	San Diego	Santa Maria	El Socorro	Guerrero Negro	San Jorge	San Carlos
<i>n</i>	26	26	62	14	46	86	10	24
Total length	6.58 ^b (±0.45)	6.32 (±0.69)	6.18 (±0.50)	6.24 (±0.55)	6.10 (±0.56)	6.56 ^b (±0.57)	7.11 ^a (±0.36)	6.78 ^a (±0.55)
Total width	3.65 ^b (±0.28)	3.50 (±0.41)	3.46 (±0.29)	3.47 (±0.28)	3.26 ^d (±0.24)	3.69 ^b (±0.30)	4.11 ^a (±0.21)	3.88 ^a (±0.33)
Pronotal width	3.04 (±0.27)	2.91 (±0.37)	2.86 (±0.27)	2.82 (±0.30)	2.69 ^b (±0.22)	3.09 (±0.26)	3.50 ^a (±0.15)	3.23 ^b (±0.30)
Posterior pronotum	2.77 (±0.25)	2.73 (±0.35)	2.64 (±0.26)	2.61 (±0.26)	2.51 ^c (±0.22)	2.93 ^c (±0.25)	3.38 ^a (±0.17)	3.13 ^b (±0.29)
Anterior pronotum	1.88 ^a (±0.15)	1.85 ^a (±0.22)	1.75 (±0.15)	1.75 (±0.17)	1.68 (±0.14)	1.92 ^a (±0.14)	1.98 ^a (±0.10)	1.88 ^a (±0.16)
Pronotal length	1.40 (±0.13)	1.35 (±0.15)	1.32 (±0.12)	1.31 (±0.15)	1.28 ^c (±0.11)	1.34 (±0.12)	1.48 ^a (±0.07)	1.40 (±0.11)
Elytral base	3.00 ^c (±0.26)	2.78 (±0.34)	2.75 (±0.25)	2.77 (±0.29)	2.59 ^d (±0.20)	3.15 ^b (±0.27)	3.51 ^a (±0.18)	3.25 ^b (±0.29)
Head width	1.64 (±0.14)	1.61 (±0.17)	1.55 (±0.13)	1.53 (±0.15)	1.47 ^b (±0.10)	1.61 (±0.11)	1.67 (±0.11)	1.67 (±0.14)

dence is consistent with the assignment of this morphotype to a single taxonomic unit. The only name available for this distinctive form is *Cryptadius sonoreae* Berry.

Figure 5 shows the character distribution of the pronotal morphometry which distinguishes the three types of *Cryptadius*. Thus evidence from both the morphometric analysis of continuous variation and the distribution of discrete characters supports the division of *Cryptadius* populations into three valid species.

Darkling beetle species are often restricted in distribution to distinctive habitats or substrates such as sand dunes, seashores or insular desert mountains. Owing to the disjunctive nature of these habitats the ranges of such species are mosaics of geographically separate demes. Isolation of these demes is intensified by the low vagility characteristic of these beetles. With the concomitant reduction in gene flow, morphological variation between demes sometimes approaches that of fully specific entities. Such vicariance is the fodder of incipient speciation, and the situation in *Cryptadius* may be indicative of a common pattern in the evolution of our North American Tenebrionidae.

KEYS AND DIAGNOSES FOR *CRYPTADIUS* AND ITS SPECIES

Genus *Cryptadius* LeConte, 1852

Diagnosis.—Flightless eurymetopines with body oblong-ovate in form, black to castaneous in color, length 5.0 to 8.2 mm. Epistomum truncate, feebly produced, often biemarginate. Gena strongly entering the eye anteriorly. Supra-orbital carina present. Outer apical angle of protibia with strongly produced, flattened, subacuminate process. Prosternum evenly deflexed behind coxae following their

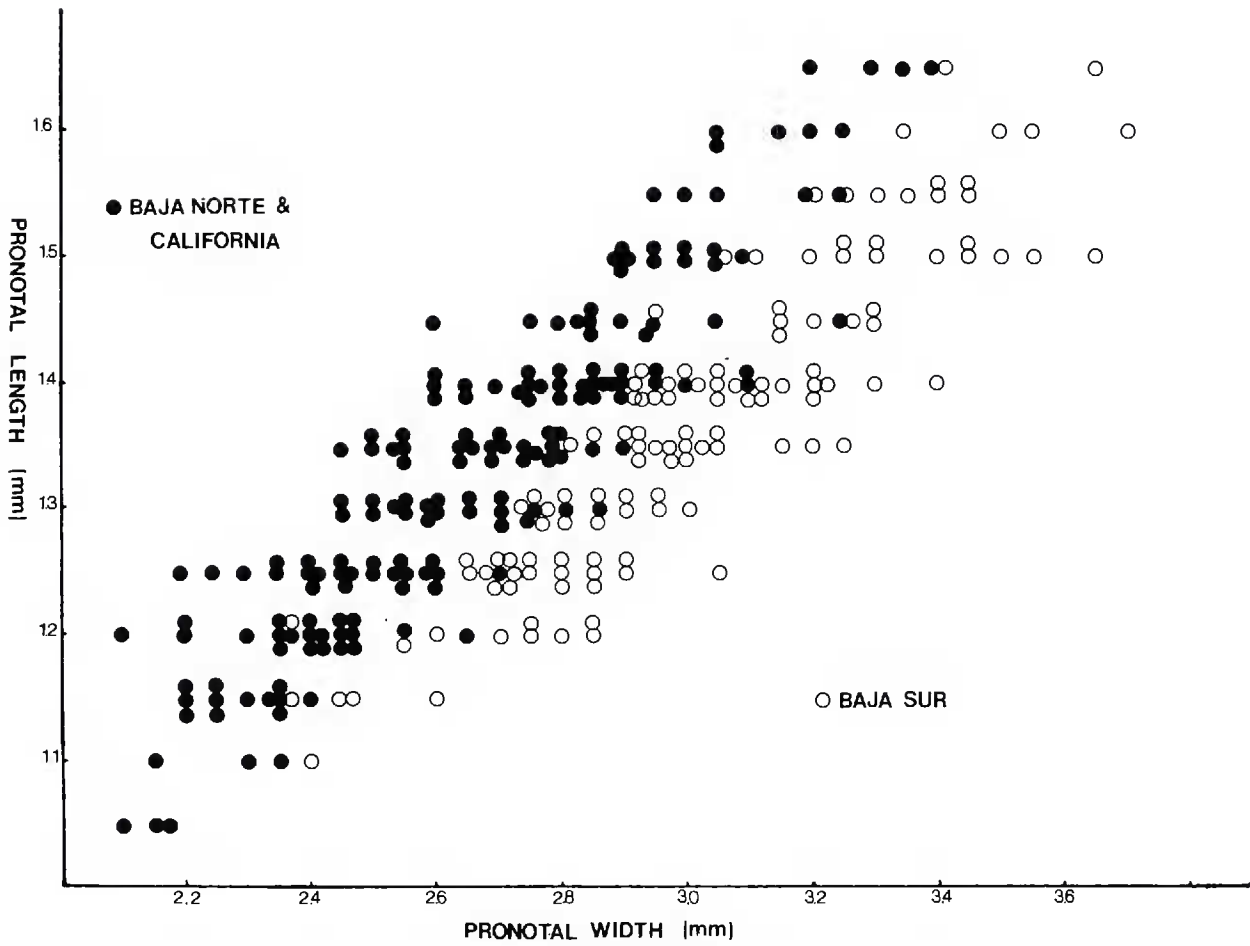


Figure 3. Pronotal proportions of *C. inflatus* expressed as mesial length vs. posterior width comparing the Pacific coast populations of Baja California Sur with those further north.

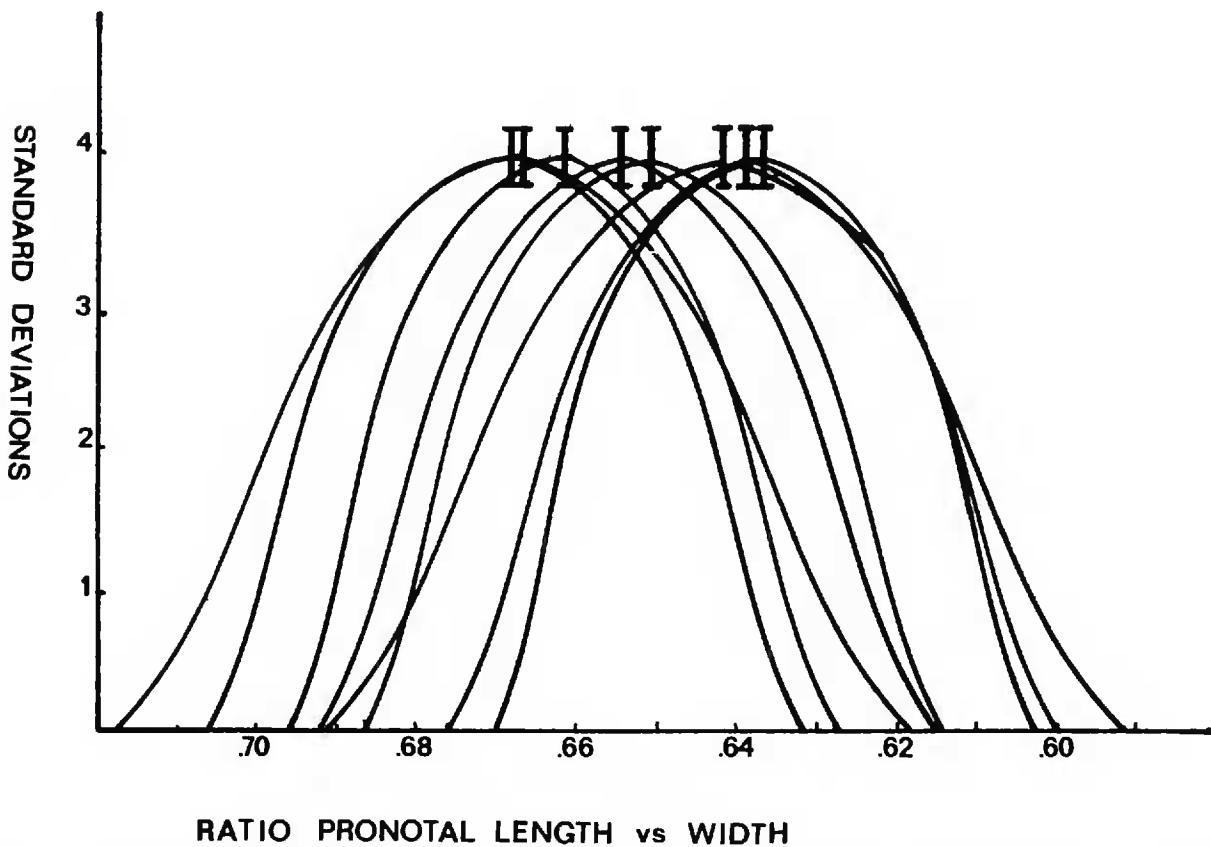


Figure 4. Variation in pronotal proportions expressed as ratio of mesial length vs. width for 8 populations of the peninsula morphotype. Area under each curve is 2 standard deviations.

Table 2. Morphometric data for gulf coast populations of *Cryptadius*,¹ localities listed from Sonora to tip of Baja peninsula. Means and standard deviations in mm. Means followed by the same letter are not significantly different at $P = 0.05$.

	Punta Chueca	Bahia Los Angeles	San Bruno	Bahia Concepcion	Playa Juncalito	Isla San Francisco	La Paz	La Ribera
<i>n</i>	38	44	16	31	16	17	39	34
Total length	7.43 ^a (±0.52)	7.03 ^b (±0.61)	7.39 ^a (±0.32)	7.83 ^c (±0.50)	7.13 ^a (±0.53)	7.30 ^a (±0.46)	7.56 ^a (±0.43)	7.57 ^a (±0.39)
Total width	3.76 ^a (±0.27)	3.52 ^b (±0.30)	3.78 ^a (±0.17)	3.90 ^a (±0.28)	3.75 ^a (±0.26)	3.78 ^a (±0.21)	3.76 ^a (±0.21)	3.70 ^a (±0.19)
Posterior pronotum	3.08 ^a (±0.22)	2.87 ^b (±0.27)	3.18 ^a (±0.16)	3.30 ^a (±0.22)	3.18 ^a (±0.25)	3.10 ^a (±0.19)	3.17 ^a (±0.21)	3.06 ^a (±0.16)
Anterior pronotum	1.99 ^a (±0.12)	1.94 ^a (±0.15)	2.11 ^a (±0.11)	2.24 ^b (±0.12)	2.07 ^a (±0.14)	2.04 ^a (±0.11)	2.05 ^a (±0.12)	2.06 ^a (±0.13)
Pronotal length	1.65 ^a (±0.10)	1.53 ^b (±0.13)	1.69 ^a (±0.12)	1.77 ^c (±0.12)	1.64 ^a (±0.10)	1.67 ^a (±0.12)	1.66 ^a (±0.09)	1.65 ^a (±0.09)
Ratio ant./post. pron.	0.646 ^a (±0.017)	0.678 ^b (±0.025)	0.664 ^c (±0.019)	0.679 ^b (±0.019)	0.651 ^{ac} (±0.025)	0.660 ^c (±0.018)	0.648 ^a (±0.019)	0.672 ^{bc} (±0.017)
Ratio L/W pronotum	0.536 ^a (±0.017)	0.533 ^a (±0.021)	0.532 ^a (±0.020)	0.537 ^a (±0.016)	0.518 ^b (±0.020)	0.539 ^a (±0.022)	0.526 ^{ab} (±0.023)	0.538 ^a (±0.017)

¹ Does not include *Cryptadius sonorae*.

contour, broadening posteriorly. Metasternum compact; distance between meso- and metacoxae less than distance from metacoxae to posterior border of first abdominal segment.

KEY TO THE SPECIES OF *CRYPTADIUS*

- 1. Posterolateral angles of pronotum obtuse, subangular to rounded 2
- Posterolateral angles of pronotum distinctly angular (gulf coast of Baja California and northern Sonora) *tarsalis* Blaisdell

Table 3. Morphometric data for *Cryptadius sonorae*. Means and standard deviations in mm.

	Punta Antonio	Punta Chueca	Guaymas	San Bruno	Bahia San Pedro ¹
<i>n</i>	1	8	21	6	1
Total length	5.80 —	6.18 (±0.34)	6.10 (±0.49)	5.99 (±0.39)	5.60 —
Total width	3.10 —	3.32 (±0.16)	3.23 (±0.29)	3.21 (±0.21)	3.20 —
Posterior pronotum	2.25 —	2.41 (±0.14)	2.38 (±0.20)	2.35 (±0.16)	2.25 —
Anterior pronotum	1.45 —	1.63 (±0.12)	1.61 (±0.13)	1.58 (±0.10)	1.55 —
Pronotal length	1.25 —	1.37 (±0.07)	1.32 (±0.12)	1.31 (±0.06)	1.30 —
Head width	1.30 —	1.37 (±0.07)	1.37 (±0.11)	1.36 (±0.07)	1.35 —

¹ Male paratype.

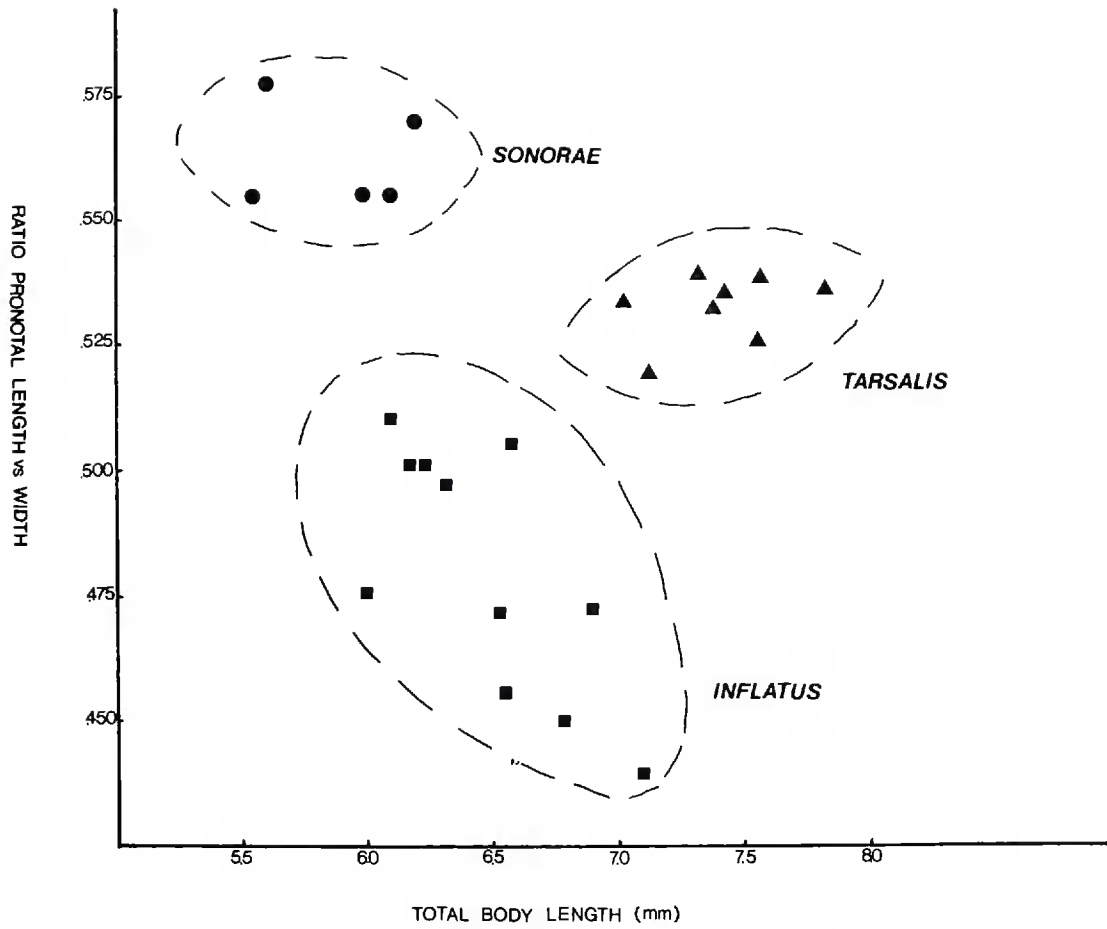


Figure 5. Scattergram of body morphometry showing clustering of mean values from different populations of *Cryptadius*.

2. Pronotum convex, narrow, embracing ventral thorax; antennae subclavate, apical segments gradually enlarged (gulf coast Sonora and Baja California) *sonorae* Berry
- Pronotum wide and depressed; antennae clavate to subcapitate, apical segments abruptly enlarged (Pacific coast of southern California and Baja California Norte) *inflatus* LeConte

***Cryptadius inflatus* LeConte, 1852**

Cryptadius inflatus LeConte, 1852. Ann. Lyceum Nat. Hist. New York, 5:140.
Eurymetopon inflatum: Casey, 1890. Ann. New York Acad. Sci., 5:346.
Cryptadius oviformis Casey, 1907. Proc. Washington Acad. Sci., 9:328.
Cryptadius punctipennis Casey, 1907. Proc. Washington Acad. Sci., 9:328.
Cryptadius curvipes Casey, 1907. Proc. Washington Acad. Sci., 9:329.

Diagnosis.—Color varying from black to pale castaneous. Posterolateral angles of pronotum rounded. Punctures on disc of pronotum mostly coalescent. Setae on pronotal margin short. Setae on epipleural margin longer but seldom exceeding width of antennal club. Antennae subcapitate, last 3 segments distinctly more robust than preceding. Epistoma biemarginate. Scutellum about equally long as wide. Aedeagus (Fig. 8) straight in lateral profile, apicale only weakly flexed.

Cryptadius inflatus inflatus LeConte, 1852. Ann. Lyceum Nat. Hist. New York, 5:140.

Length usually less than 6.8 mm, averaging ca. 6.5 mm. Pronotum evenly convex; posterolateral angles broadly rounded. Ratio of mesial length to posterior width of pronotum 0.47 to 0.55 (*n* = 183).

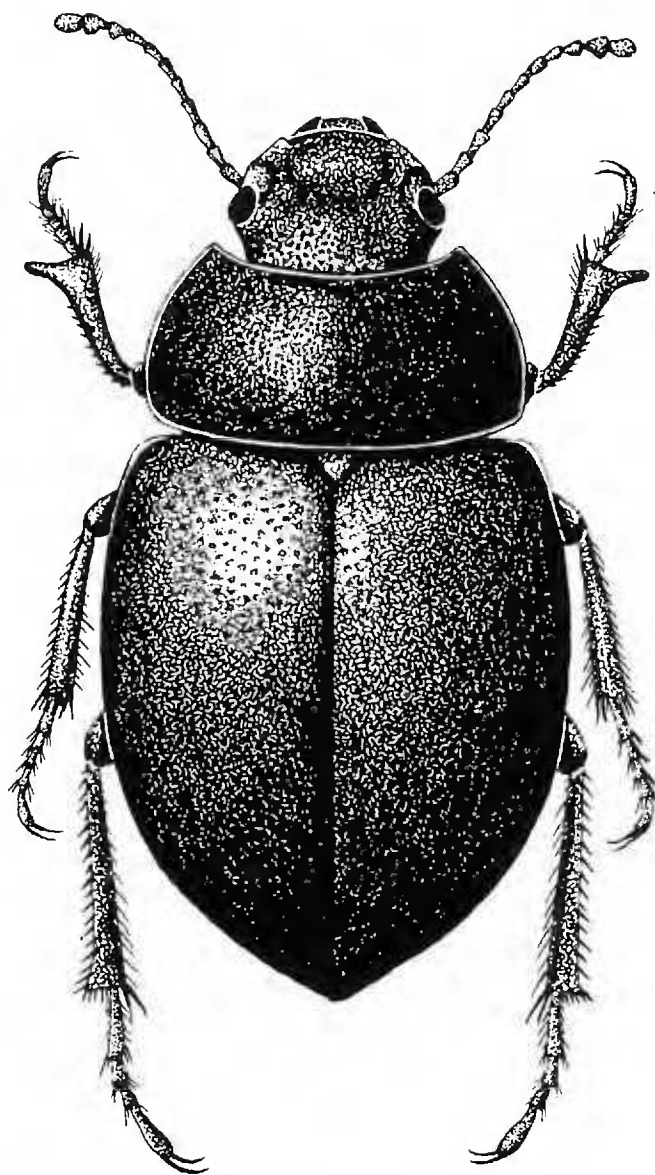


Figure 6. *Cryptadius inflatus blaisdelli*, new subspecies; dorsal facies.

Distribution and habitat.—Pacific coast of southern California from Pt. Conception and Santa Cruz Island south to El Rosario, Baja California Norte. Found on coastal strands in beach sand beneath littoral vegetation such as *Salicornia*, *Mesembranthemum* and *Abronia*.

***Cryptadius inflatus blaisdelli*, NEW SUBSPECIES**

(Fig. 6)

Length usually more than 6.7 mm, averaging ca. 7.0 mm. Pronotum depressed; posterolateral angles narrowly rounded, though not angular. Ratio of length to posterior width of pronotum 0.42 to 0.48 ($n = 125$).

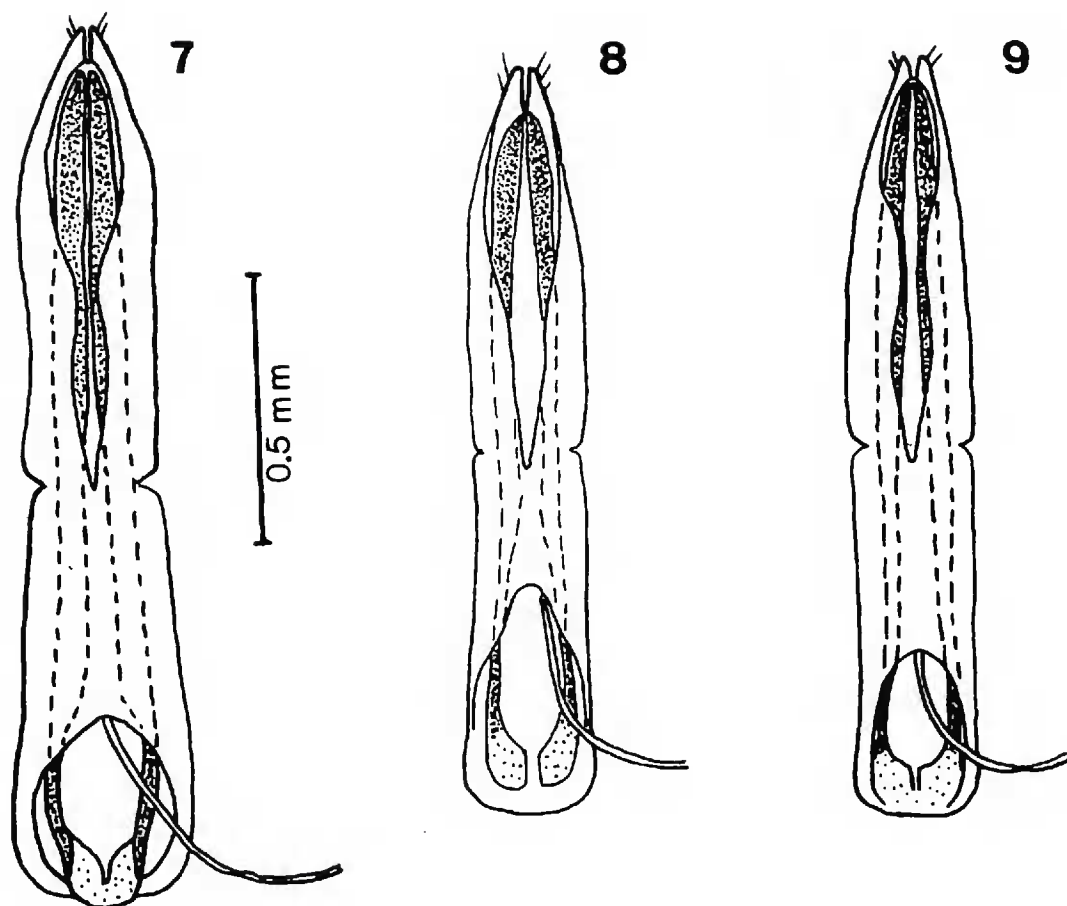
Distribution and habitat.—Pacific coast of Baja California Sur as far north as Guerrero Negro. Found on coastal strands in beach sand beneath littoral vegetation such as *Salicornia*.

Holotype.—♂; MEXICO, Baja California Sur, Las Barrancas. 5 Sept. 1983. D. B. Thomas & C. A. Olson. Deposited California Academy of Science.

Paratypes.—24 specimens labeled same as holotype. Deposited California Academy of Science, University of Arizona and collection of author.

Additional material examined from Baja California Sur: Guerrero Negro, San Jorge, San Carlos, Punta Conejo, Playa Migrino, Playa Los Cerritos, Isla Asuncion, Isla Natividad and Isla San Roque.

Comment.—The distributions of the two subspecies converge just north of Guerrero Negro. A series of specimens from Millers Landing, Baja California



Figures 7-9. Aedeagi of *Cryptadius* species, dorsal view. 7. *C. tarsalis*. 8. *C. inflatus*. 9. *C. sonorae*.

Norte, show intergradation in character and none are typical of either subspecies. The pronotum is depressed as in *blaisdelli*, but the body size is small as in *inflatus*. Further the pronotal ratio among these specimens varies from 0.45 to 0.51, which is intermediate to and overlapping the typical forms of the two races.

***Cryptadius tarsalis* Blaisdell, 1923**

Cryptadius tarsalis Blaisdell, 1923. Proc. California Acad. Sci., 12:212.

Cryptadius angulatus Blaisdell, 1923. Proc. California Acad. Sci., 12:210.

Cryptadius sinuatus Blaisdell, 1923. Proc. California Acad. Sci., 12:211.

Cryptadius andrewsi Berry, 1977. Proc. Entomol. Soc. Washington, 79:561.

Diagnosis.—Color black to castaneous. Posterolateral angles of pronotum distinctly angular; punctations on disc of pronotum mostly discrete. Scutellum much wider than long. Antennae subclavate, apical segments only gradually enlarging. Setae on epipleural margin short, length about equal to distance between them. Aedeagus (Fig. 7) distinctly bent in lateral view.

Distribution and habitat.—Gulf coast of the Baja California peninsula and northern Sonora. Also on Isla Santa Catalina, Isla San Francisco, Isla Carmen, Isla San Jose, Isla Espiritus Santo and Isla Coronado. Found on coastal strands in beach sand under *Salicornia*, *Mesembrantherum*, *Frankenia*, *Proboscidea* and *Atriplex*.

***Cryptadius sonorae* Berry, 1974**

Cryptadius sonorae Berry, 1974. Proc. Entomol. Soc. Washington, 76:175.

Diagnosis.—Color castaneous to pale castaneous. Pronotum proportionately narrow and convex, embracing ventral thorax; posterolateral angles obtuse, weakly angular; punctation on disc dense but shallow. Scutellum wider than long. Epi-

pleural and pronotal margin with long golden setae, longer than distance separating them, and those on epipleural margin longer than width of antennae. Epistoma feebly biemarginate. Antennae subclavate, the apical segments gradually enlarging. Aedeagus (Fig. 9) nearly straight in lateral profile, apex only weakly flexed.

Distribution and habitat.—Gulf coast of Sonora from Punta Peñasco to Huatabampo and at one location in Baja California Sur, Playa San Bruno. Occurs on coastal strands in beach sand under *Salicornia*, *Frankenia* and *Abronia*.

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